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Molecular Phylogenetics of *Phalaenopsis* (Orchidaceae) and allied Genera: Re-evaluation of Generic Concepts

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Molecular phylogenetic analyses were performed using data sets derived from DNA sequences of the plastid genome (*matK* and *trnK* introns) and the nuclear genome (rDNA ITS) in an examination of relationships of all sections of *Phalaenopsis* and closely related genera. The following insights were provided: (1) The genera *Lesliea* and *Nothodoritis* are nested within *Phalaenopsis*. (2) *Phalaenopsis* subgenus *Aphyllae* and section *Esmeralda*, often treated as the independent genera *Kingidium* and *Doritis* respectively, are also nested within *Phalaenopsis*. (3) Two subgenera of *Phalaenopsis*, namely, *Phalaenopsis* and *Parishianae*, are not monophyletic. (4) *Phalaenopsis* sections *Deliciosae*, *Stauroglottis*, *Amboinenses* and *Zebrinae* are not monophyletic. (5) Inconsistencies between the plastid and nuclear lineages indicate a hybrid origin of P*halaenopsis minus* and *Phalaenopsis philippinensis*. (6) In light of these findings, and to accommodate phylogenetic integrity and stability in nomenclature, we adopt a broadly defined *Doritis* characterized by the possession of four pollinia, an explicit character state.

Key words: *Doritis*, introgression, ITS, *matK*, molecular, Orchidaceae, *Phalaenopsis*, phylogenetics, *trnK*

Phalaenopsis Blume is an orchid genus to which 62 species are currently assigned (Christenson 2001). According to Dressler's classification of the Orchidaceae (1993), the genus belongs to subfamily Epidendroideae Lindl. tribe Vandeae Lindl. subtribe Aeridinae Pfitzer. The genus occurs from southern India and Sri Lanka in the west to New Guinea and northern Australia in the east. It extends as far north as southern China and Taiwan. The center of diversity of the genus is Borneo, from where 13 species are currently known.

Several monographic treatments of the genus have been published notably by Rolfe (1886), Sweet (1968-69, 1980) and Christenson (2001). Shim (1984) revised the generic classification with emphasis on floral morphology. The history of classification of the genus has been thoroughly reviewed by Sweet (1980). In the present study, we follow the system proposed by Christenson (2001) as this work incorporates the most recent data (Table 1). In his revision, Christenson (2001) treated *Phalaenopsis* in a broad sense, sinking the genera *Doritis* Lindl. and *Kingidium* P. F. Hunt, both of which have been treated as independent genera by other authors (*e.g.* Seidenfaden 1988, Dressler 1993), into *Phalaenopsis*.

This major inconsistency among taxonomists is largely due to different weighting attributed to the critical morphological character, pollinium number. Although pollinium number has traditionally been considered a heavily weighted character in the classification of orchid genera, its state is not uni-

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TABLE 1. Species of *Phalaenopsis* and allied genera used for *matK-trnK* introns and ITS sequencing. Infrageneric classification follows Christenson (2001).

Species	Voucher
Subgenus *Proboscidioides* (Rolfe) Christenson	
Phalaenopsis lowii Rchb. f.	*TBG 144316**
Subgenus *Aphyllae* (H. R. Sweet) Christenson	
Phalaenopsis braceana (Hook. f.) Christenson	*TBG 144566*
Phalaenopsis minus (Seidenf.) Christenson	*TBG 145839*
Phalaenopsis wilsonii Rolfe	*TBG 144214*
Phalaenopsis sp.	*Yukawa 29689*
Subgenus *Parishianae* (H. R. Sweet) Christenson	
Phalaenopsis appendiculata C. E. Carr	*TBG 144305*
Phalaenopsis lobbii (Rchb. f.) Sweet	*TBG 78865*
Phalaenopsis parishii Rchb. f.	*TBG 133881*
Subgenus *Polychilos* (Breda) Christenson	
Section *Polychilos* (Breda) Christenson	
Phalaenopsis cornu-cervi (Breda) Blume & Rchb. f.	*TBG 145696*
Phalaenopsis mannii Rchb. f.	*TBG 118380*
Phalaenopsis pantherina Rchb. f.	*Tsukahara s. n.*
Section *Fuscatae* H. R. Sweet	
Phalaenopsis cochlearis Holttum	*TBG 144209*
Phalaenopsis kunstleri Hook. f.	*TBG 137083*
Phalaenopsis viridis J. J. Sm.	*TBG 141055*
Phalaenopsis sp.	*TBG 142238*
Section *Amboinenses* H. R. Sweet	
Phalaenopsis amboinensis J. J. Sm.	*TBG 133762*
Phalaenopsis bastianii Gruss & Röllke	*TBG 140637*
Phalaenopsis bellina (Rchb. f.) Christenson	*TBG 118533*
Phalaenopsis doweryënsis Garay & Christenson	*TBG 144564*
Phalaenopsis fasciata Rchb. f.	*TBG 145726*
Phalaenopsis fimbriata J. J. Sm. subsp. *sumatrana* (J. J. Sm.) Christenson	*TBG 145860*
Phalaenopsis floresensis Fowlie	*TBG 145748*
Phalaenopsis gigantea J. J. Sm.	*TBG 137307*
Phalaenopsis hieroglyphica (Rchb. f.) H. R. Sweet	*TBG 145743*
Phalaenopsis javanica J. J. Sm.	*TBG 145868*
Phalaenopsis lueddemanniana Rchb. f.	*TBG 145733*
Phalaenopsis lueddemanniana Rchb. f. var. *ochracea* Rchb. f.	*TBG 145863*
Phalaenopsis maculata Rchb. f.	*TBG 144569*
Phalaenopsis mariae Burb. ex R. Warneer & B. S. Williams	*TBG 141056*
Phalaenopsis micholitzii Rolfe	*TBG 140566*
Phalaenopsis modesta J. J. Sm.	*TBG 140664*
Phalaenopsis pallens (Lindl.) Rchb. f.	*TBG 145744*
Phalaenopsis pulchra (Rchb. f.) H. R. Sweet	*TBG 145761*
Phalaenopsis reichenbachiana Rchb. f. & Sander	*TBG 145875*
Phalaenopsis venosa Shim & Fowlie	*TBG 145770*
Phalaenopsis violacea Witte	*TBG 145785*
Section *Zebrinae* Pfitzer	
Phalaenopsis inscriptiosinensis Fowlie	*TBG 144571*
Phalaenopsis sumatrana Korth. & Rchb. f.	*TBG 142440*
Phalaenopsis tetraspis Rchb. f.	*TBG 145841*

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TABLE 1. (continued).

Species	Voucher
Subgenus *Phalaenopsis*	
Section *Phalaenopsis*	
Phalaenopsis amabilis (L.) Blume	*TBG 145847*
Phalaenopsis amabilis (L.) Blume subsp. *rosenstromii* (F. M. Bailey) Christenson	*TBG 140318*
Phalaenopsis aphrodite Rchb. f. (1)	*TBG 141408*
Phalaenopsis aphrodite Rchb. f. (2)	*TBG 141151*
Phalaenopsis philippinensis Golamco ex Fowlie & Tang	*TBG 118882*
Phalaenopsis sanderiana Rchb. f.	*Atagawa s. n.*
Phalaenopsis schilleriana Rchb. f.	*HBG 0309*
Phalaenopsis stuartiana Rchb. f.	*TBG 145758*
Section *Deliciosae* Christenson	
Phalaenopsis chibae T. Yukawa	*TBG 115846*
Phalaenopsis deliciosa Rchb. f. (1)	*TBG 145842*
Phalaenopsis deliciosa Rchb. f. (2)	*TBG 144594*
Section *Esmeralda* Rchb. f.	
Phalaenopsis pulcherrima (Lindl.) J. J. Sm.	*TBG 118342*
Phalaenopsis sp. "buyssoniana"	*TBG 145823*
Section *Stauroglottis* (Schauer) Benth.	
Phalaenopsis equestris (Schauer) Rchb. f.	*TBG 141154*
Phalaenopsis celebensis H. R. Sweet	*TBG 145822*
Phalaenopsis lindenii Loher	*TBG 140568*
Allied taxa	
Lesliea mirabilis Seidenf.	*TBG 145844*
Nothodoritis zhejiangensis Z. H. Tsi	*TBG 137501*
Outgroup	
Amesiella monticola J. E. Cootes & D. P. Banks	*TBG 123790*

*TBG series indicate accession numbers in living collection database at Tsukuba Botanical Garden.

form within *Phalaenopsis*. The predominant number in the genus is two, but the subgenera *Proboscidioides*, *Aphyllae* and *Parishianae* all have four pollinia, as do the sections *Deliciosae* and *Esmeralda* (both in subgenus *Phalaenopsis*). Immense diversity in the structure of reproductive organs, particularly that of the labellum and the stipe, has also resulted in inconsistent interpretations of relationships in the group.

Phalaenopsis also exhibits remarkable diversity in terms of ecology. Most species are epiphytes, though the species of section *Esmeralda* have a terrestrial life form. On the other hand, plants in subgenera *Aphyllae*, *Parishianae* and *Proboscidioides* shed their leaves during the dry season.

Phylogentic relationships in *Phalaenopsis* remain largely unresolved. Woodward (1951), Sagawa (1962), Shindo & Kamemoto (1963), Sagawa & Shoji (1968), Arends (1970), Shoji (1976, 1980), Aoyama (1993), Aoyama *et al.* (1994) and Kao *et al.* (2001) investigated cytological characters, Brandange *et al.* (1971, 1972) examined alkaloid content and Tsai *et al.* (2003) conducted a molecular phylogenetic analysis of the internal transcribed spacer regions of the 18S-26S nuclear ribosomal DNA (ITS) in subgenus *Phalaenopsis*. In the present study, we compared and combined DNA sequences of a maturase-encoding gene (*matK*) flanked by

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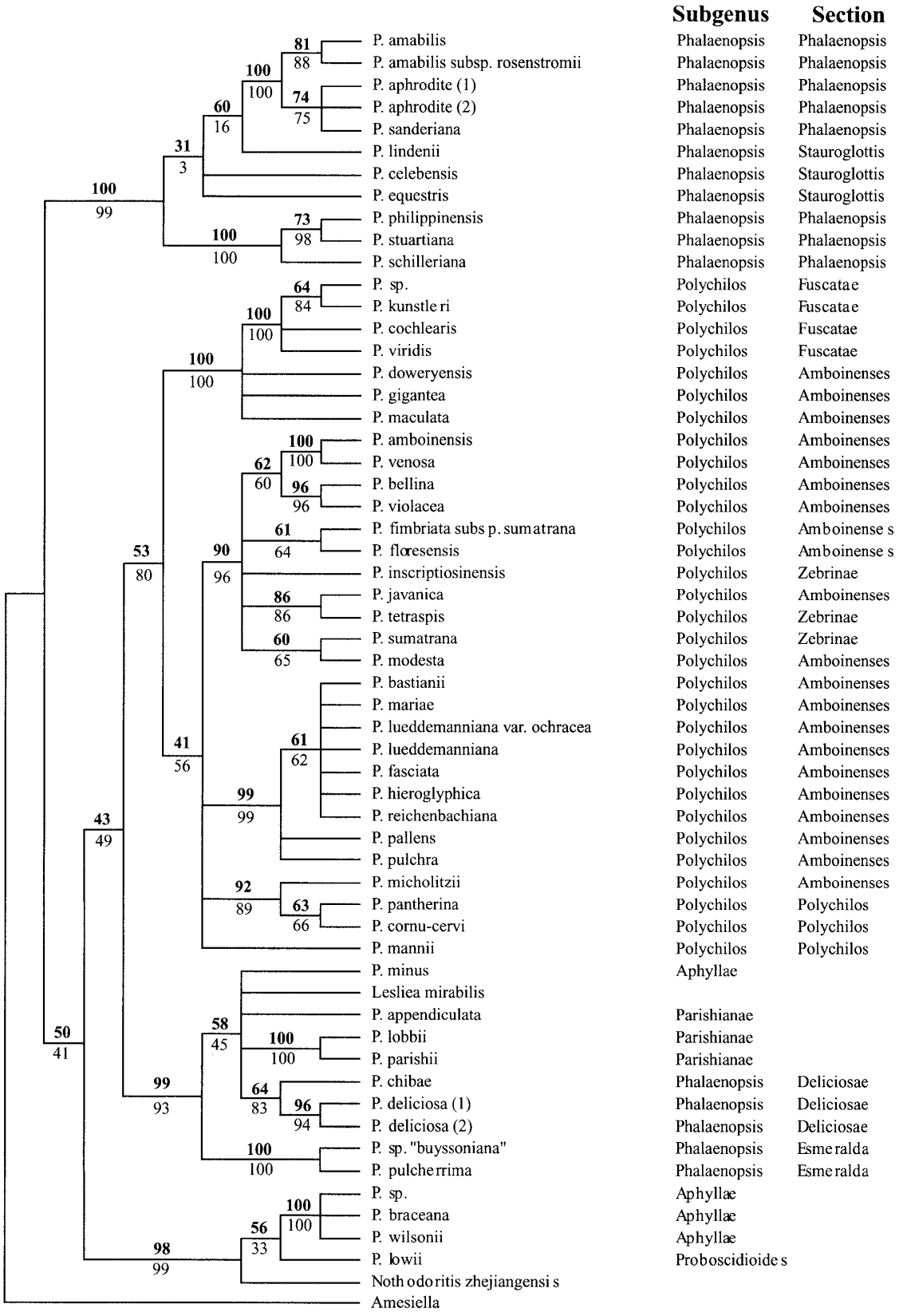

FIG. 1. Strict consensus of 24 most-parsimonious Fitch trees based upon *matK-trnK* introns sequences: length=593, consistency index=0.7808 (0.6328 excluding uninformative characters), retention index of 0.8751. Numbers above internodes indicate bootstrap values from 1,000 replicates of Fitch parsimony analysis (maxtree limit of 1,000 per replicate). Numbers below internodes indicate bootstrap values from 1,000 replicates of neighbor-joining distance analysis.

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introns of the plastid gene *trnK*, the *trnK* introns and the ITS region from members of all sections of *Phalaenopsis* and closely related genera to clarify relationships within the genus.

Materials and Methods

We selected 53 representative taxa from all subgenera and sections of *Phalaenopsis* for inclusion in the study. *Lesliea* Seidenf. and *Nothodoritis* Z. H. Tsi were also included in the study because morphological characters of these two genera suggest a close relationships with *Phalaenopsis* (Christenson 2001). *Paraphalaenopsis* A. D. Hawkes, a genus also regarded as being closely related to *Phalaenopsis*, was not included in the study because an earlier comprehensive molecular analysis of subtribe Aeridinae had revealed wide phylogenetic separation between the two (Topik *et al.*, in press). Based on the results of the same analyses, *Amesiella* Garay was chosen as the outgroup taxon. Table 1 lists the materials used in the phylogenetic analysis. Voucher specimens have been deposited at TNS.

Experimental methods followed those described in Yukawa *et al.* (1993, 1996). Sequences were determined by amplifying *matK*, *trnK* introns and the ITS region (including 5.8S rDNA and parts of 18S and 26S rDNA) via the polymerase chain reaction (PCR) from a total DNA extract. PCR primers were as given in Yukawa *et al.* (1999) for the *matK-trnK* 3' intron and as in Douzery *et al.* (1999) for ITS. We developed the following combination of primers for the trnK 5' intron: 3914FN: 5'-ATCTGGGTTGCTAACTCAATGG-3' and OMAT1R: 5'-CAATATGGTCAGAACGGCGT-3'. DNA sequences were aligned manually. Gaps were treated as missing characters. The aligned data file is available from the first author upon request. Parsimony and distance analyses were conducted with PAUP* version 4.0b6 (Swofford 2001). The heuristic option was used to perform Fitch parsimony analyses (Fitch 1971). Branch lengths for trees were calculated using ACCTRAN optimization (Swofford & Maddison 1987). Distance trees were obtained using the neighbor-joining (NJ) method (Saitou & Nei 1987) with a Kimura two-parameter correction (Kimura 1980). To assess the relative robustness for branches, the bootstrap method (Felsenstein 1985) was used with 1000 replicates.

Results

Figure 1 shows a strict consensus of 24 most parsimonious (MP) trees derived from the *matK-trnK* introns sequences. The tree had a consistency index (CI) of 0.7808 (0.6328 excluding uninformative characters) and a retention index (RI) of 0.8751. In this data set topologies with more than 50% bootstrap support were nearly identical between MP and NJ analyses (Fig. 1), though section *Stauroglottis* formed a sister group with three species of section *Phalaenopsis* (*P. philippinensis*, *P. schilleriana* and *P. stuartiana*) in the NJ tree (83% bootstrap support).

A strict consensus of 322 MP trees on the basis of the ITS data set is shown in Fig. 2. For this tree, CI was 0.5521 (0.4770 excluding uninformative characters) and RI was 0.8169; topologies with more than 50% bootstrap support were nearly identical between MP and NJ analyses (Fig. 2), although the monophyly of two individuals of *Phalaenopsis aphrodite* was well supported only in NJ analysis (86% bootstrap support).

Analyses of *matK-trnK* introns sequences provided results substantially concordant with those achieved via analyses of ITS sequences, except for the positions of *Phalaenopsis philippinensis* and *P. minus*. In the plastid phylogeny, *P. philippinensis* formed a sister group with *P. stuartiana*; in the nuclear phylogeny, *P. philippinensis* was nested between the *P. stuartiana-schilleriana* clade and the *P. amabilis-aphrodite-sanderiana* clade. Likewise, the plastid phylogeny supported placement of *P. minus* in a clade comprising *Lesliea* and

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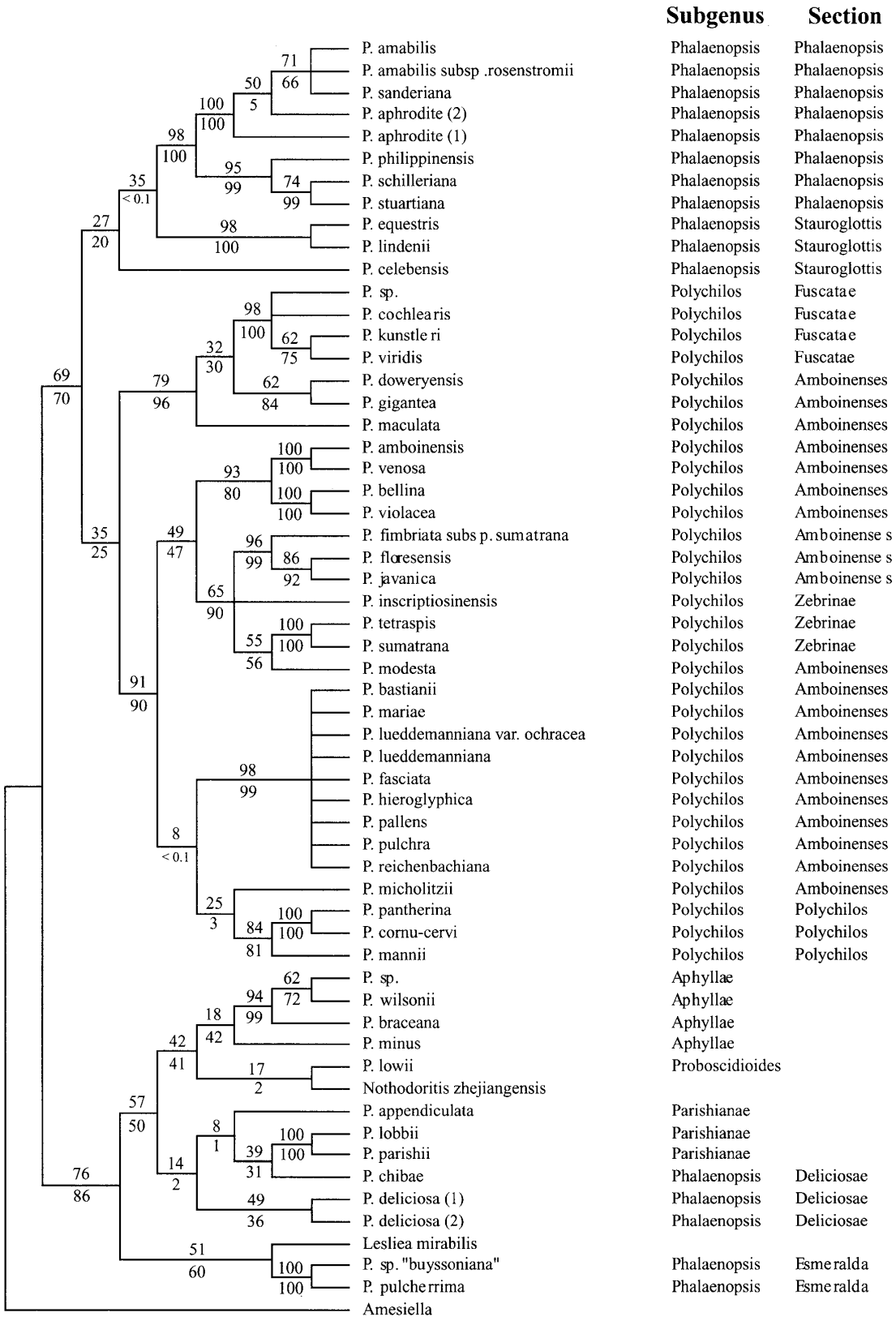

FIG. 2. Strict consensus of 322 most-parsimonious Fitch trees based upon ITS sequences: length=585, consistency index=0.5521 (0.4770 excluding uninformative characters), retention index of 0.8169. Numbers above internodes indicate bootstrap values from 1,000 replicates of Fitch parsimony analysis (maxtree limit of 1,000 per replicate). Numbers below internodes indicate bootstrap values from 1,000 replicates of neighbor-joining distance analysis.

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Phalaenopsis subgenera *Parishianae* and *Phalaenopsis* sections *Deliciosae* and *Esmeralda*, whereas the nuclear phylogeny indicated a nested position in a clade formed of *Nothodoritis* and *Phalaenopsis* subgenera *Aphyllae* and *Proboscidioides*.

In such cases, analyses of combined data sets excluding problematic taxa provide more resolution and internal support for relationships than do individual data sets (*e.g.*, Olmstead & Sweere 1995, Wongsawad *et al.* 2001, Yukawa 2001, Yukawa *et al.* 2002). We thus conducted a combined analysis of the information derived from *matK-trnK* introns and ITS sequences. In this analysis *Phalaenopsis philippinensis* and *P. minus* were excluded. The length of the aligned sequence was 3768 base pairs. Figure 3 shows a strict consensus of 896 MP trees from the combined data set. CI was 0.6557 (0.5296 excluding uninformative characters) and RI was 0.8297. In this data set, topologies with more than 50% bootstrap support were almost identical between the MP and NJ analyses (Fig. 3), although *P. celebensis* formed the basal position in the clade comprising *Phalaenopsis* sections *Phalaenopsis* and *Stauroglottis* in the MP analysis, whilst it was nested between *Phalaenopsis* sections *Phalaenopsis* and *Stauroglottis* in the NJ analysis.

In the combined analysis, the following insights were provided (Fig. 3): (1) the genera *Lesliea* and *Nothodoritis* are nested within the genus *Phalaenopsis*. (2) *Phalaenopsis* subgenus *Aphyllae* and section *Esmeralda*, often treated as the independent genera *Kingidium* and *Doritis* respectively, are also nested within *Phalaenopsis*. (3) *Phalaenopsis* subgenera *Phalaenopsis* and *Parishianae* are not monophyletic. (4) *Phalaenopsis* sections *Deliciosae*, *Stauroglottis*, *Amboinenses* and *Zebrinae* are not monophyletic. (5) The genus *Phalaenopsis* is apparently composed of two major clades, here termed Clade 1 and Clade 2.

Discussion

Biogeography

The two major clades recognized in this study are characterized by markedly different patterns in geographical distribution of their constituent species. Thus species in Clade 1 are mostly distributed within the limits of Malesia, as defined by van Steenis (1950). The few exceptions are as follows: *Phalaenopsis aphrodite* (section *Phalaenopsis*), which is known from the Philippines and Taiwan; *P. amabilis* (section *Phalaenopsis*), widely dispersed throughout the Malesian region, though its range extends also into northern Australia; *P. cornu-cervi* (section *Polychilos*), also very widely distributed, occurring from northeastern India to Java and Borneo; and *P. mannii* (section *Polychilos*), a close relative of *P. cornu-cervi* found throughout the Himalayas and in Indochina. *P. mannii* is the only species in Clade 1 that occurs exclusively outside the Malesian region. In contrast, species in Clade 2 are particularly diverse in the Himalayas, southern China and Indochina. However, there are a few exceptions: *P. pulcherrima* (section *Esmeralda*), which also occurs in Sumatra and Borneo; *P. deliciosa* (section *Deliciosae*), the most widely-distributed species in the genus with a range that extends from Sri Lanka and India to the Philippines and Sulawesi; *P. mysorensis* (section *Deliciosae*), a species with an isolated distribution in southern India; and *P. appendiculata* (subgenus *Parishianae*), a species recorded from the Malay Peninsula and as such the only "Malesian" member of this clade.

This distinction in geographical distribution indicates that speciation within Clade 1 has occurred mostly in Malesia, whilst that in Clade 2 has occurred predominantly in the Himalayan and Indochinese regions. In an attempt to explain this pattern, two competing hypotheses are proposed.

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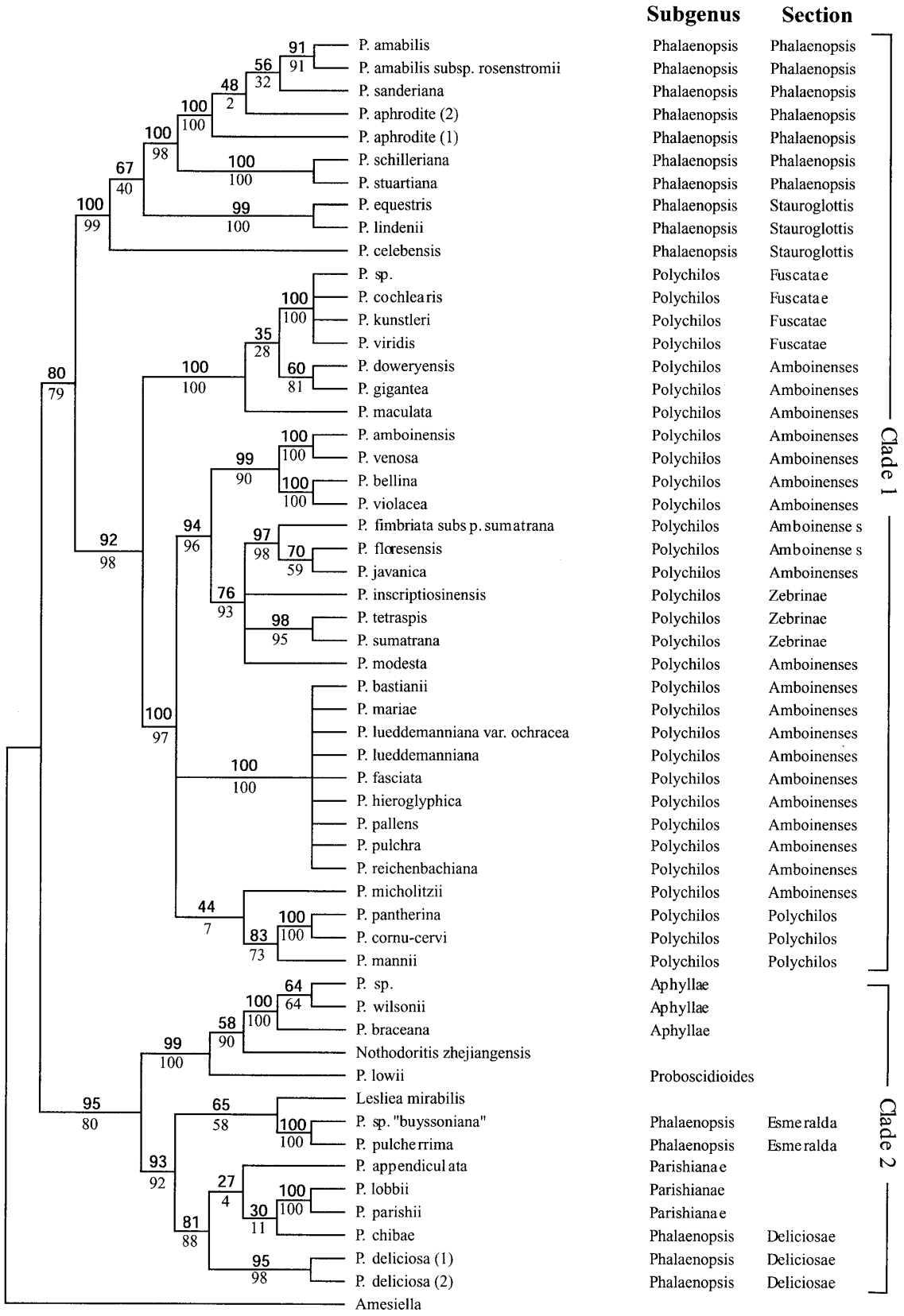

FIG. 3. Strict consensus of 896 most-parsimonious Fitch trees based upon *matK-trnK* introns and ITS sequences: length=1153, consistency index=0.6557 (0.5296 excluding uninformative characters), retention index of 0.8297. Numbers above internodes indicate bootstrap values from 1,000 replicates of Fitch parsimony analysis (maxtree limit of 1,000 per replicate). Numbers below internodes indicate bootstrap values from 1,000 replicates of neighbor-joining distance analysis.

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The first invokes cladogenesis of two precursor lineages, with subsequent radiation occurring in each lineage relatively recently. Prior to cladogenesis, the only available corridor linking the two lineages in the Malesian and Indochinese regions was the Malay Peninsula, and, consequently, dispersal between the two regions was rare.

The second hypothesis emphasizes environmental differences between the Malesian and Indochinese regions in demarcating the observed distribution patterns of Clades 1 and 2. The climate of the Malesian region is characterized by rather constant, high precipitation throughout the year. In contrast, the Indochinese region has a marked dry season. Ancestral stocks in each major clade may have adapted exclusively to one or other of these environmental conditions, with subsequent divergence being reinforced through elaboration of specialized functions in either lineage.

There are three major reasons why the first hypothesis should be rejected. First, pair-wise distances of nucleotide divergence between the two major clades and taxa in each clade are great. For example, the divergence between *Phalaenopsis equestris* in Clade 1 and *P. pulcherrima* in Clade 2 in ITS sequences is 8.7%. Consequently, it is not plausible to hypothesize a recent origin of the two major clades and subsequent radiation in each clade. Second, corridors linking the Malesian and Indochinese regions were much wider during glacial periods in the Pleistocene (Morley & Flenley 1987). Thus geographical barriers between the two regions are negligible, if we take account the time-scale required for speciation. Third, long-distance wind dispersal of orchid seeds is frequent (*e.g.,* Gandawijaja & Arditti 1983). The occurrence of *P. aphrodite* in both the Philippines and Taiwan provides a good example of long-distance dispersal because there is no geologic evidence for a past land connection between Taiwan and the northern Philippines during the Tertiary (Tan 2002).

On the other hand, morphological evolution of vegetative organs in *Phalaenopsis* and allies correlates with pronounced environmental differences between the Malesian and Indochinese regions. For instance, in Clade 1, species in sections *Amboinenses*, *Fuscatae* and *Zebrinae* occur in evergreen forests under low light levels (Christenson 2001) where the leaves do not have to endure prolonged periods in a desiccating environment (K. Suzuki, personal communication). In contrast, species in section *Polychilos* have succulent leaves adapted to bright places high in the forest canopy (Christenson 2001, T. Yukawa, unpublished data). Accordingly, they are likely to have been able to extend the distribution to the Indochinese region where a definite dry season exists. In Clade 2, members of *Phalaenopsis* subgenera *Aphyllae*, *Parishianae* and *Proboscidioides* and the genus *Nothodoritis* shed their leaves during the dry season. It is interesting to note that the distributions of these taxa largely overlap with areas of subtropical monsoon climate where pine-deciduous *Dipterocarpus* forest and lower montane pine-oak forest dominate (Santisuk 1988). As such, the deciduous habit in these groups likely represents an adaptation to a seasonally severe water deficit. Moreover, these groups have developed green, flattened roots that serve as a photosynthetic organ particularly during the deciduous period (Benzing *et al.* 1983). Species with vegetative organs suited to specialized ecological and physiological conditions would be less likely to be able to establish in niches in markedly different climate regimes. We thus support the second hypothesis that attaches importance to environmental factors for the advent of a bimodal distribution pattern within *Phalaenopsis*.

Morphology of reproductive organs

The enormous morphological diversification of reproductive organs in subtribe Aeridiinae is well documented in studies based both on morphological (*e.g.,* Seidenfaden 1988) and macromolecular characters (Topik *et al.* in press).

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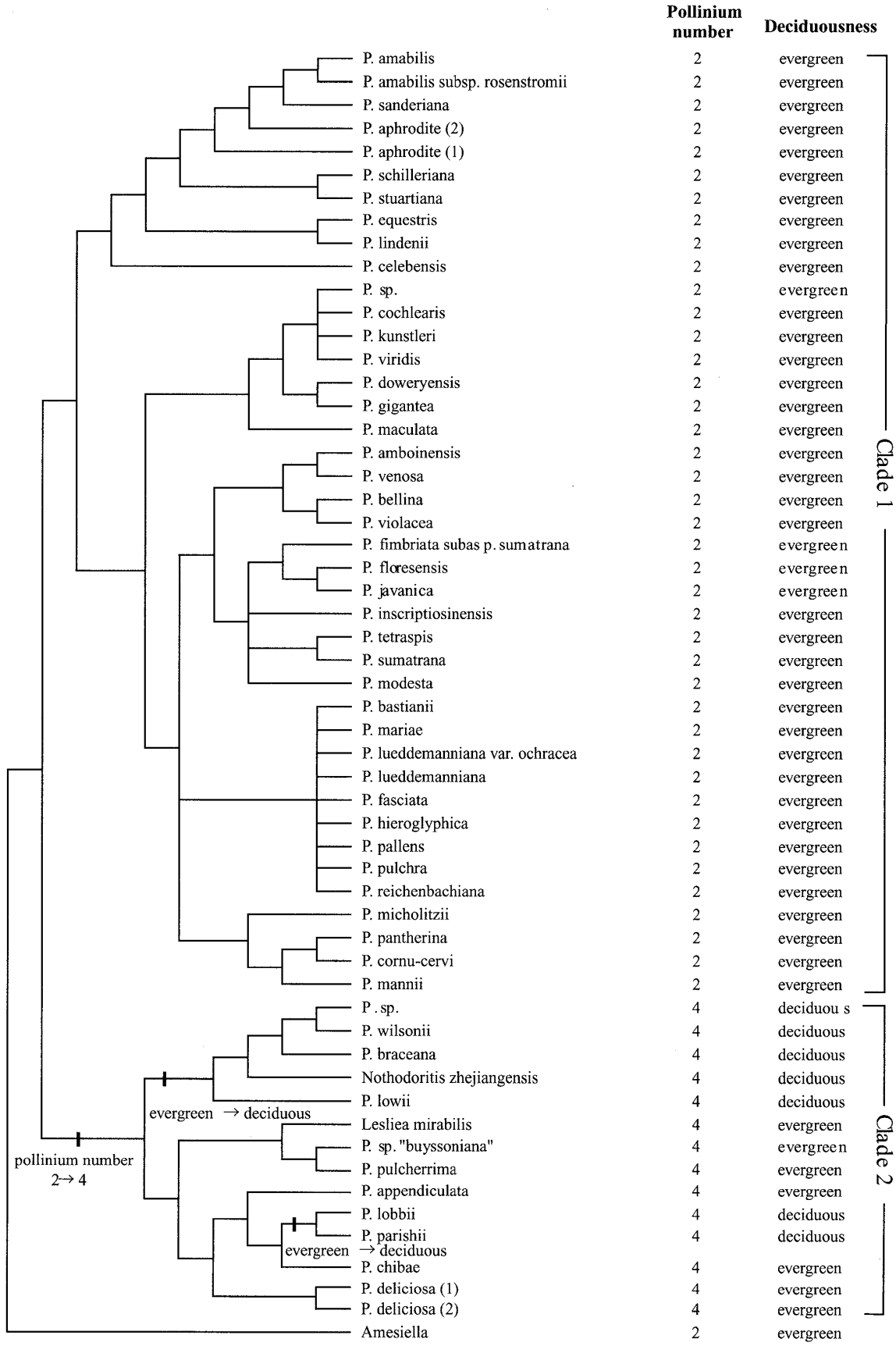

FIG. 4. Reconstruction of evolution in pollinium number and deciduousness in *Phalaenopsis* and allied genera under ACCTRAN optimization. The tree is the strict consensus Fitch tree based upon *matK-trnK* introns and ITS sequences.

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The most controversial character in the classification of *Phalaenopsis* and allies is the number of pollinia (2 or 4) among the members. Part of *Phalaenopsis* subgenus *Phalaenopsis* (*i.e.*, sections *Phalaenopsis* and *Stauroglottis*) and *Phalaenopsis* subgenus *Polychilos* have two pollinia. However, the remainder of *Phalaenopsis*, *Lesliea* and *Nothodoritis* have four pollinia (Fig. 4). The most parsimonious reconstruction of pollinium number in subtribe Aeridinae based on a molecular phylogenetic tree indicated that the apomorphic state in the *Phalaenopsis* group is four (Topik *et al.* in press), this state having arisen once in the lineage leading to Clade 2, namely, *Phalaenopsis* subgenera *Phalaenopsis* (sections *Deliciosae* and *Esmeralda* only), *Aphyllae*, *Parishianae* and *Proboscidioides*, *Lesliea* and *Nothodoritis* (Fig. 4).

Since the pollinium number of Orchidaceae is usually considered to be stable, and because it has been treated as a cardinal character among taxonomists, the variability in this genus has provoked much discussion (*e.g.*, Yukawa 1996, Christenson 2001). Our results indicate that the conservative nature of pollinium number is not a rule but a "dogma" in orchid classification. Actually, variation in pollinium number is found in other small- to medium-sized monophyletic groups such as *Thunia* Rchb. f. (*e.g.*, Seidenfaden 1986) and *Cymbidium* Sw. (*e.g.*, Yukawa *et al.* 2002).

Other reproductive characters such as structures of the labellum and the stipe are much diversified in this group. Emphasis of such characters has formed the basis for circumscription of small-sized genera such as *Doritis* (in a narrow sense; equivalent to *Phalaenopsis* section *Esmeralda* in this study), *Kingidium* (in a narrow sense; equivalent to *Phalaenopsis* subgenus *Aphyllae* in this study), *Nothodoritis* and *Lesliea*. *Doritis* (in a narrow sense) has the following apomorphies: long column-foot (about as long as the column), elongate stipe, two linear appendages at the basal part of the labellum and four globular pollinia. An obscure to prominent spur of the labellum, chlorophyllous perianth lobes, four subglobular pollinia and a deciduous habit unite *Kingidium* (in a narrow sense). *Nothodoritis* is characterized by an appendaged column, an elongate stipe, two sub-oblong appendages at the basal part of the labellum, four subglobular pollinia and a deciduous habit. A column with three calli at the base, a tubular stipe with a flange separating each pair of pollinia, four subglobular pollinia and an operculum with teeth at the front characterize *Lesliea*. Establishment of new genera based solely on their specialized character states may result in para-/polyphyly of closely related genera, if synapomorphies which specifically unite their sister groups are not found. In this case, such morphological synapomorphies of the sister group of each segregated genus do not exist. Actually, our molecular data definitely corroborate the paraphyly of *Phalaenopsis*, if we accept *Doritis* (in a narrow sense), *Kingidium* (in a narrow sense), *Nothodoritis* and *Lesliea* at generic level.

Morphology of vegetative organs

Phalaenopsis and allied genera comprise both evergreen and deciduous species. *Phalaenopsis* subgenera *Aphyllae*, *Parishianae* (except for *P. appendiculata*) and *Proboscidioides*, as well as the genus *Nothodoritis*, shed their leaves during the dry season (Fig. 4). As mentioned above, the deciduous habit in this group likely represents an adaptation to a seasonally severe water deficit. The results of this study suggest that deciduousness likely evolved twice—once in the lineage leading to *Phalaenopsis* subgenus *Parishianae* (excluding *P. appendiculata*) and once in the common ancestor of *Phalaenopsis* subgenera *Aphyllae* and *Proboscidioides* and genus *Nothodoritis* (Fig. 4). In association with this character evolution, these groups developed green, flattened roots which serve as a photosynthetic organ particularly during the dry period when the plant sheds its leaves. Benzing *et al.* (1983) showed that roots of the deciduous *P. taenialis* (subgenus

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Aphyllae) have thinner velamina with a decreased number of layers, a larger volume of cortical intercellular space, and more elaborate aeration tissues than the leafy *P. amabilis* (section *Phalaenopsis*) and outgroup genera. It is clear that these anatomical alterations facilitate gaseous exchanges in the roots.

Life form

Since every sister group candidate to *Phalaenopsis* is epiphytic (Topik *et al.* in press), the terrestrial life form in *Phalaenopsis* section *Esmeralda* represents an apomorphic state that arose only once in this group. Recent phylogenetic analyses have clarified that the Orchidaceae has a terrestrial ancestry (Neyland & Urbatsch 1995, Cameron *et al.* 1999). Therefore, evolution from the epiphytic to terrestrial life form in *Phalaenopsis* represents a reversal in the Orchidaceae as a whole. Yukawa *et al.* (2002) found the same reversal pattern in another orchid genus, *Cymbidium*. These results indicate that the changes in life forms are not necessarily rare evolutionary events within the Orchidaceae.

The shift to a terrestrial life form in *Phalaenopsis* section *Esmeralda* accompanies several morphological changes. Comparisons of anatomical characters of roots in *Phalaenopsis* revealed that *Phalaenopsis* section *Esmeralda* has more numbers of velamen cell layers (T. Yukawa & H. Motomura, unpublished data) than the epiphytic species. Moreover, *Phalaenopsis* section *Esmeralda* has cylindrical roots and never exhibits dorsiventrality, as is found in epiphytic *Phalaenopsis* species. It seems clear that the attached roots of epiphytic orchids are absorptive, and that absorption is promoted by thick velamina (Pridgeon 1987). The C3 photosynthesis of epiphytic roots in *Phalaenopsis* has been documented by Endo & Ikushima (1989). The dorsiventral roots, therefore, are adaptations to photosynthesis and water absorption on bark. Based on these facts, it is likely that changes in above-mentioned character states correlate with a shift in life forms. Furthermore, the erect inflorescence in *Phalaenopsis* section *Esmeralda* is also an exceptional character state in the genus, since all other species of *Phalaenopsis* have patent to pendulous inflorescences. There is no doubt that the erect inflorescence represents another adaptation to the terrestrial life form.

Cytological characters

As suggested by Woodward (1951), Sagawa (1962), Shindo & Kamemoto (1963), Sagawa & Shoji (1968), Shoji (1976, 1980), and Aoyama (1993), *Phalaenopsis* shows a consistent somatic chromosome number of 38, except for the tetraploid species, *P.* sp. "*buysonniana*" and a few chance polyploid individuals. In the genus, Shindo & Kamemoto (1963) found the following karyomorphological diversification: *Phalaenopsis amabilis* (section *Phalaenopsis*), *P. schilleriana* (section *Phalaenopsis*), *P. equestris* (section *Stauroglottis*), *P. lindenii* (section *Stauroglottis*) and *P. lueddemanniana* (section *Amboinenses*) have small chromosomes and relatively symmetrical karyotypes. On the other hand, *P. pulcherrima* (section *Esmeralda*), *P. mannii* (section *Polychilos*) and *P. violacea* (section *Amboinenses*) have 2 to 3 times larger and less symmetrical chromosomes than the first group. Similar karyomorphological diversification has been described by Shoji (1976), Aoyama (1993) and Kao *et al.* (2001). Although these data do not reflect the full species diversity of the genus, several evolutionary trends can be hypothesized. Both larger and smaller sizes of chromosomes characterizing several *Phalaenopsis* species might have been derived from medium size chromosomes, which are characteristic of most members of subtribe *Aeridinae*, the outgroup of *Phalaenopsis* (Shindo & Kamemoto 1963). The results of our phylogenetic analyses indicate that a clade comprising sections *Phalaenopsis* and *Stauroglottis* is characterized by small chromosomes and that a clade in section *Amboinenses* including *P. amboinensis*, *P. venosa* and *P. violacea* is characterized by large chromo-

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somes. On the other hand, we found that *P. cornucervi* and *P. mannii* show a close affinity, though their chromosome sizes are greatly differentiated as indicated by Shoji (1976). These data may suggest that evolutionary changes in chromosome size can occur within a short period of time.

Arends (1970) and Aoyama *et al.* (1994) observed the frequency of normal and irregular microspores in artificially-raised F_1 hybrids of *Phalaenopsis* and suggested correlations between genome affinity and karyomorphology. The data revealed that intrasectional hybrids of sections *Phalaenopsis*, *Polychilos* and *Stauroglottis*, and other intersectional hybrids such as *Phalaenopsis-Stauroglottis*, *Amboinenses-Polychilos* and *Esmeralda-Parishianae* have high percentages of normal microspores. Arends (1970) further studied chromosome associations at metaphase I of F_1 hybrids of *Phalaenopsis*. He found that intrasectional hybrids of section *Phalaenopsis* and intersectional hybrids of *Phalaenopsis-Stauroglottis* and *Amboinenses-Polychilos* show high levels of meiotic chromosome homology whereas intersectional hybrids such as *Amboinenses-Stauroglottis*, *Amboinenses-Phalaenopsis* and *Polychilos-Stauroglottis* exhibit low levels of meiotic chromosome homology. These results are also consistent with the phylogenetic affinities inferred in the present study.

Inconsistencies between plastid and nuclear lineages

We found a discrepancy in the placement of *Phalaenopsis philippinensis* and *P. minus* between *matK-trnK* introns and ITS trees. There are two scenarios to describe inconsistent phylogenetic positions for these two species: one is caused by acceleration of nucleotide substitution rates in the samples concerned and the other is due to introgressions.

The first scenario is based on the notion that higher rates of nucleotide substitution in a particular lineage tend to draw inaccurate phylogenetic estimation in the parsimony analysis (Felsenstein 1978). The relative rate test was conducted for the above-mentioned two species both in *matK-trnK* introns and ITS sequences. Since constancy of substitution rates was not rejected in these samples ($P<0.01$; results not shown), it is not probable that the first scenario caused the discrepancy.

Introgressions, the second scenario, are more plausible to describe the phylogenetic descrepancy in the two species. In the Philippines, there are several records of natural hybrids involving species in section *Phalaenopsis*, such as *P.* ×*amphitrite* Kraenzl. (putative parents: *P. sanderiana* and *P. stuartiana*), *P.* ×*intermedia* Lindl. (putative parents: *P. aphrodite* and *P. equestris*), *P.* ×*leucorrhoda* Rchb. f. (putative parents: *P. aphrodite* and *P. schilleriana*), and *P.* ×*veitchiana* Rchb. f. (putative parents: *P. equestris* and *P. schilleriana*). The sister group relationship between *P. philippinensis* and *P. stuartiana* in the plastid phylogeny indicates that the maternal stock of *P. philippinensis* could be an ancestral species of *P. stuartiana* because maternal inheritance of plastid DNA has been confirmed in the Orchidaceae (Corriveau & Coleman 1988, Sears 1980). However, it is unlikely that the latter is a direct parent of *P. philippinensis* because the native habitat of *P. stuartiana* is more than 1100km distant from that of *P. philippinensis*, and because the divergence in *matK-trnK* introns was 5 substitutions plus 2 insertions/deletions between the two species. A nested position of *P. philippinensis* between the *P. stuartiana-schilleriana* clade and the *P. amabilis-aphrodite-sanderiana* clade in the nuclear phylogeny may indicate a hybrid origin for this species between these two clades. If this hypothesis is correct, the paternal parent is assumed to be a species in the *P. amabilis-aphrodite-sanderiana* clade.

Owing to its peculiar morphological characters in reproductive organs, the phylogenetic position of *Phalaenopsis minus* has remained unresolved. Christenson (2001) argued in favor of its placement in subgenus *Aphyllae* because the presence of a shallow depression underneath the posterior callus

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of the labellum is a character that shares with members of subgenus *Aphyllae*. Since the plastid phylogeny showed that *P. minus* is definitely grouped within a clade comprising *Lesliea* and *Phalaenopsis* subgenera *Parishianae* and *Phalaenopsis* sections *Deliciosae* and *Esmeralda*, the maternal parent must be a member of this clade. *Phalaenopsis minus* has a restricted distribution in north and upper northeast Thailand where *L. mirabilis*, *P. parishii* (subgenus *Parishianae*), *P. deliciosa* (section *Deliciosae*) and *P. pulcherrima* (section *Esmeralda*) also occur. The mother species or intermediates thereof, however, are assumed to be extinct or as yet undiscovered because the known members of this clade exhibit considerable genetic divergence with *P. minus* (*e.g.*, 24 substitutions and 3 insertions/deletions between *P. minus* and *P. deliciosa* in *matK-trnK* introns). On the other hand, the nuclear phylogeny indicates a nested position of *P. minus* between the above-mentioned clade and subgenus *Aphyllae*. This suggests that the paternal parent of *P. minus* belongs to subgenus *Aphyllae*, a proposition supported by the presence of a depression on the labellum in both. If the species *P. tanialis*, the sole representative of this subgenus in Thailand, were included in the analysis, a more robust concept of the parentage of *P. minus* would likely be established.

Reclassification of the genus

Progressing from the above discussion of morphological characters, it seems straightforward to recognize several small-sized genera within this group. As already stated, however, such treatments result in para-/polyphyly of *Phalaenopsis*. Based on the circumscription of *Phalaenopsis* by Christenson (2001), the genus becomes a paraphyletic group because *Lesliea* and *Nothodoritis* are nested within *Phalaenopsis*. There are two alternatives for the restoration of monophyly in *Phalaenopsis*: one is to define *Phalaenopsis* in a broad sense. In this option, *Lesliea* and *Nothodoritis* are sunk into *Phalaenopsis*. The other is to circumscribe *Phalaenopsis* in a narrow sense. In this option, there are several logical solutions: for example, Clade 1 can be defined as *Phalaenopsis* because it includes the type species, *P. amabilis*. The broadest circumscription of Clade 2 is to define the clade as a single genus. In this case, *Doritis* becomes the correct name because this is the oldest available name. On the other hand, to preserve *Lesliea* and *Nothodoritis* at generic level, it becomes necessary to instate several subclades of Clade 2 at generic level.

To choose a single classification system among several phylogenetically correct resolutions, priority should be placed on nomenclatural stability consistent with the scientific evidence and without the superfluous creation of names, as clearly stated in the Preamble of the International Code of Botanical Nomenclature (Greuter *et al.* 2000). As recognized widely, *Phalaenopsis* and *Doritaenopsis* (a nothogenus between *Phalaenopsis* and *Doritis*) are important ornamental crops with more than 24,000 nothotaxa. Given this fact, the inclusion of *Doritis* in *Phalaenopsis* would necessitate a lot of name changes. We therefore contend that a broad definition of *Phalaenopsis* (to include *Doritis*) would violate the aim of nomenclatural stability.

As mentioned above, the recognition of subclades in Clade 2 at generic level necessitates the establishment of several new genera. For example, if we conserve the genus *Nothodoritis*, *Phalaenopsis lowii* should be treated as a monotypic genus. Since there are no appropriate available names for *P. lowii* as a monotypic genus, a new generic name would be needed. We hesitate to establish more small-sized genera in subtribe Aeridinae. Furthermore, several relationships within Clade 2 are only moderately supported by bootstrap analyses. Very narrow generic concepts in Clade 2 are, therefore, not preferable.

Kingidium P. F. Hunt was also sunk into *Phalaenopsis* by Christenson (2001). However, a generic definition of *Kingidium* has yet to be stabilized. If the genus is treated in the broadest sense,

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Phalaenopsis subgenus *Aphyllae* and subgenus *Phalaenopsis* section *Deliciosae* correspond to *Kingidium*. *Phalaenopsis* subgenus *Aphyllae* is equivalent to *Kingidium* in a narrow sense because Hunt (1971) selected *Aerides taeniale* Lindl. as the lectotype of the genus *Kingidium*. Our results demonstrate that *Phalaenopsis* subgenus *Aphyllae* and subgenus *Phalaenopsis* section *Deliciosae* occupy distant subclades in Clade 2. Consequently, if we maintain *Kingidium* in a classification of this group, we have to deal with it in the narrow sense. A definition of *Kingidium* based on synapomorphic morphological characters is difficult. An apparent synapomorphy is the distinct spur, though this is lacking in *P. wilsonii*. On the other hand, several species in other subclades in Clade 2, such as *P. chibae*, *P. deliciosa* and *Lesliea*, possess a spur. Leaf deciduousness during the dry season also characterizes *Kingidium* in the narrow sense, but this character state is also found in *Phalaenopsis* subgenera *Parishianae* and *Proboscidioides*, and the genus *Nothodoritis*. Owing to the lack of good synapomorphic morphological characters, we therefore hesitate in resurrecting the genus *Kingidium* in our system.

After re-examination of morphological characters in Clade 2, we conclude that it is not possible to characterize every subclade using unambiguous synapomorphies. Clade 2 as a whole, however, can be characterized by a distinct synapomorphy, four pollinia. Since this character state is an explicit one, circumscription of Clade 2 as a single independent genus is the most reasonable solution. As mentioned above, we can apply a single generic name, *Doritis*, to all taxa in Clade 2. Some name changes are inevitable with this option, but we can conserve established uses of *Doritis*, *Doritaenopsis*, and other inter-generic hybrids using *Doritis*, in this way. Christenson (2001)'s broad concept of *Phalaenopsis* was based on phylogenetic trees available at that time (D. Jarrell, unpublished data). These trees suggested that the establishment of *Doritis* at generic level violates the monophyly of *Phalaenopsis*. Increased sampling and additional molecular characters in this study provide evidence of more robust relationships and the results show that both *Phalaenopsis* and *Doritis* can be conserved in an appropriate manner.

Owing to their conflicting positions in the plastid and nuclear lineages, *Phalaenopsis philippinensis* and *P. minus* were excluded from the combined analysis. However, the placement of *P. philippinensis* in Clade 1 and *P. minus* in Clade 2 is unambiguous because inconsistencies of these species occur within each major clade.

In accordance with this treatment, the circumscription of genus *Phalaenopsis* corresponds to Clade 1. Our results show that several parts of Christenson's infrageneric classification of *Phalaenopsis* (2001) are in need of revision. At subgeneric level, subgenus *Phalaenopsis* becomes monophyletic provided that sections *Deliciosae* and *Esmeralda* are transferred to *Doritis*. The monophyly of subgenus *Polychilos* is also well supported. However, at sectional level, section *Amboinenses* is paraphyletic because sections *Fuscatae*, *Polychilos* and *Zebrinae* are nested within it. Furthermore, sections *Stauroglottis* and *Zebrinae* may prove to be polyphyletic. Weak to moderate support of several subclades in this study indicates that more molecular evidence is needed to clarify sectional relationships in *Phalaenopsis*. We therefore treat the genus *Phalaenopsis* as comprising two subgenera, namely, *Phalaenopsis* and *Polychilos*, without further subdivision. In conclusion, we advocate the following revised system, largely in accordance with a widely applied concept of *Phalaenopsis* and closely related genera without major name changes.

Taxonomy

Nomenclatural changes

Doritis appendiculata (C. E. Carr) T. Yukawa & K. Kita, **comb. nov.**

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Basionym: *Phalaenopsis appendiculata* C. E. Carr, Gard. Bull. Straits Settlem. 5: 16 (1929).

Synonym: *Polychilos appendiculata* (C. E. Carr) Shim, Malayan Nat. J. 36: 24 (1982).

Doritis chibae (T. Yukawa) T. Yukawa & K. Kita, **comb. nov.**

Basionym: *Phalaenopsis chibae* T. Yukawa, Ann. Tsukuba Bot. Gard. 15: 19 (1996).

Synonym: *Kingidium chibae* (T. Yukawa) Gruss & Röllke, Orchidee (Hamburg) 48: 261 (1997).

Doritis deliciosa (Rchb. f.) T. Yukawa & K. Kita, **comb. nov.**

Basionym: *Phalaenopsis deliciosa* Rchb. f., Bonplandia 2: 93 (1854).

Synonyms: *Kingidium deliciosum* (Rchb. f.) H. R. Sweet, Amer. Orchid Soc. Bull. 39: 1095 (1970).

Aerides latifolia Thwaites, Enum. Pl. Zeyl. 429 (1861); *Doritis latifolia* (Thwaites) Trimen. Cat. 89 (1885).

Phalaenopsis bella Teijsm. & Binn., Natuurk. Tijdschr. Ned.-Indié 24: 321 (1862); *Kingidium deliciosum* var. *bellum* (Teijsm. & Binn.) Gruss & Röllke, Orchidee (Hamburg) 44: 225 (1993).

Phalaenopsis hebe Rchb. f., Hamburger Garten-Blumenzeitung 18: 35 (1862); *Doritis hebe* (Rchb. f.) Schltr., Repert. Spec. Nov. Rengni Veg. Beih. 1: 968 (1913); *Kingiella hebe* (Rchb. f.) Rolfe, Orchid Rev. 25: 197 (1917).

Phalaenopsis wightii Rchb. f., Bot. Zeitung (Berlin) 20: 214 (1862); *Doritis wightii* (Rchb. f.) Benth. & Hook. f., Gen. Pl. 3: 574 (1883); *Kingidium wightii* (Rchb. f.) Gruss & Röllke, Orchidee (Hamburg) 46: 23 (1995).

Phalaenopsis amethystina Rchb. f., Gard. Chron. 1865: 602 (1865).

Phalaenopsis alboviolacea Ridl., Trans. Linn. Soc. London, Bot., ser. 2, 3: 373 (1893).

Doritis philippinensis Ames, Orchid. 2: 235 (1908); *Kingiella philippinensis* (Ames) Rolfe, Orchid Rev. 25: 197 (1917).

Doritis steffensii Schltr., Repert. Spec. Nov. Regni Veg. 10: 194 (1911).

Phalaenopsis hebe var. *amboinensis* J. J. Sm., Philipp. J. Sci. 12: 260 (1917).

Doritis deliciosa subsp. **hookeriana** (Gruss & Röllke) T. Yukawa & K. Kita, **comb. nov.**

Basionym: *Kingidium hookerianum* Gruss & Röllke, Orchidee (Hamburg) 46: 23 (1995).

Synonym: *Phalaenopsis deliciosa* subsp. *hookeriana* (Gruss & Röllke) Christenson, *Phalaenopsis*. A Monograph, 223 (2001).

Doritis gibbosa (H. R. Sweet) T. Yukawa & K. Kita, **comb. nov.**

Basionym: *Phalaenopsis gibbosa* H. R. Sweet, Amer. Orchid Soc. Bull. 39: 1095 (1970).

Synonym: *Polychilos gibbosa* (H. R. Sweet) Shim, Malayan Nat. J. 36: 25 (1982).

Doritis hainanensis (T. Tang & F. T. Wang) T. Yukawa & K. Kita, **comb. nov.**

Basionym: *Phalaenopsis hainanensis* T. Tang & F. T. Wang, Acta Phytotax. Sin. 12: 47 (1974).

Synonym: *Phalaenopsis chuxiongensis* F. Y. Liu, Acta Bot. Yunnan. 18: 411 (1996).

Doritis honghenensis (F. Y. Liu) T. Yukawa & K. Kita, **comb. nov.**

Basionym: *Phalaenopsis honghenensis* F. Y. Liu, Acta Bot. Yunnan. 13: 373 (1991).

Doritis lobbii (Rchb. f.) T. Yukawa & K. Kita, **comb. nov.**

Basionym: *Phalaenopsis parishii* var. *lobbii* Rchb. f., Refug. Bot. 2: sub t. 85 (1870).

Synonyms: *Phalaenopsis lobbii* (Rchb. f.) H. R. Sweet, Genus *Phalaenopsis*, 53 (1980); *Polychilos lobbii* (Rchb. f.) Shim, Malayan Nat. J. 36: 25 (1982).

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Phalaenopsis listeri Berkeley, Gard. Chron., ser. 3, 1: 280 (1887), nom. nud.

Doritis lobbii f. **flava** (Gruss & Röllke ex Christenson) T. Yukawa & K. Kita, **comb. nov.**

Basionym: *Phalaenopsis parishii* var. *lobbii* f. *flava* Gruss & Röllke ex Christenson, *Phalaenopsis*. A Monograph, 71 (2001).

Synonym: *Phalaenopsis lobbii* f. *flava* (Gruss & Röllke ex Christenson) Christenson, *Phalaenopsis*. A Monograph, 71 (2001).

Doritis lobbii f. **flavilabia** (Christenson) T. Yukawa & K. Kita, **comb. nov.**

Basionym: *Phalaenopsis lobbii* f. *flavilabia* Christenson, *Phalaenopsis*. A Monograph, 72 (2001).

Doritis lowii (Rchb. f.) T. Yukawa & K. Kita, **comb. nov.**

Basionym: *Phalaenopsis lowii* Rchb. f., Bot. Zeitung (Berlin) 20: 214 (1862).

Synonyms: *Polychilos lowii* (Rchb. f.) Shim, Malayan Nat. J. 36: 24 (1982).

Phalaenopsis proboscidioides Parish ex Rchb. f., Xenia Orchid. 2: 139 (1868), nom. nud.

Doritis minus (Seidenf.) T. Yukawa & K. Kita, **comb. nov.**

Basionym: *Kingidium minus* Seidenf., Opera Bot. 95: 188 (1988).

Synonym: *Phalaenopsis minus* (Seidenf.) Christenson, *Phalaenopsis*. A Monograph, 54 (2001).

Doritis mirabilis (Seidenf.) T. Yukawa & K. Kita, **comb. nov.**

Basionym: *Lesliea mirabilis* Seidenf., Opera Bot. 95: 190 (1988).

Doritis mysorensis (Saldanha) T. Yukawa & K. Kita, **comb. nov.**

Basionym: *Phalaenopsis mysorensis* Saldanha, Indian Forester 100: 572 (1974).

Synonyms: *Kingidium mysorensis* (Saldanha) Sathish, Cat. Indian Orchid., 95 (1994).

Kingidium niveum Sathish, Cat. Indian Orchid., 53 (1994).

Doritis parishii (Rchb. f.) T. Yukawa & K. Kita, **comb. nov.**

Basionym: *Phalaenopsis parishii* Rchb. f., Bot. Zeitung (Berlin) 23: 146 (1865).

Synonyms: *Grafia parishii* (Rchb. f.) A. D. Hawkes, Phytologia 13: 306 (1966); *Polychilos parishii* (Rchb. f.) Shim, Malayan Nat. J. 36: 26 (1982).

Aerides decumbens Griff., Notul. Pl. Asiat. 3: 365 (1851), nomen confusum.

Doritis stobartiana (Rchb. f.) T. Yukawa & K. Kita, **comb. nov.**

Basionym: *Phalaenopsis stobartiana* Rchb. f., Gard. Chron., n. s., 8: 392 (1877).

Synonyms: *Phalaenopsis wightii* var. *stobartiana* (Rchb. f.) Burb., The Garden 22: 19 (1882); *Kingidium stobartianum* (Rchb. f.) Seidenf., Opera Bot. 95: 188 (1988).

Doritis wilsonii (Rolfe) T. Yukawa & K. Kita, **comb. nov.**

Basionym: *Phalaenopsis wilsonii* Rolfe, Kew Bull. 1909: 65 (1909).

Synonym: *Phalaenopsis minor* F. Y. Liu, Acta Bot. Yunnan. 10: 119 (1988).

Doritis zhejiangensis (Z. H. Tsi) T. Yukawa & K. Kita, **comb. nov.**

Basionym: *Nothodoritis zhejiangensis* Z. H. Tsi, Acta Phytotax. Sin. 27: 59 (1989).

Revised classification of Phalaenopsis *and allied genera*

Phalaenopsis Blume, Bijdr. 7: 294 (1825). *Type*

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species: *Epidendrum amabile* L.

Subgenus **Phalaenopsis**

Phalaenopsis amabilis (L.) Blume, Bijdr. 7: 294 (1825).

Phalaenopsis ×amphitrite Kraenzl., Gard. Chron., ser. 3, 11: 618 (1892).

Phalaenopsis aphrodite Rchb. f., Hamburger Garten-Blumenzeitung 18: 35 (1862).

Phalaenopsis celebensis H. R. Sweet, Genus *Phalaenopsis*, 66 (1980).

Phalaenopsis equestris (Schauer) Rchb. f., Linnaea 22: 864 (1850).

Phalaenopsis ×intermedia Lindl., Paxton's Fl. Gard. 3: 162 (1853).

Phalaenopsis ×leucorrhoda Rchb. f., Gard. Chron., n. s., 3: 301 (1875).

Phalaenopsis lindenii Loher, J. Orchidees 6: 103 (1895).

Phalaenopsis philippinensis Golamco ex Fowlie & Tang, Orchid Digest 51: 92 (1987).

Phalaenopsis sanderiana Rchb. f., Flora 65: 466 (1882).

Phalaenopsis schilleriana Rchb. f., Hamburger Garten-Blumenzeitung 16: 115 (1860).

Phalaenopsis stuartiana Rchb. f., Gard. Chron., n. s., 16: 748 (1881).

Phalaenopsis ×veitchiana Rchb. f., Gard. Chron. 1872: 935 (1872).

Subgenus **Polychilos** (Breda) Christenson, *Phalaenopsis*. A Monograph, 76 (2001). *Type species*: *Polychilos cornu-cervi* Breda.

Phalaenopsis amboinensis J. J. Sm., Bull. Dép. Agric. Indes. Néerl. 45: 23 (1911).

Phalaenopsis bastianii Gruss & Röllke, Orchidee (Hamburg) 42: 76 (1991).

Phalaenopsis bellina (Rchb. f.) Christenson, Brittonia 47: 58 (1995).

Phalaenopsis borneënsis Garay, Lindleyana 10: 182 (1995).

Phalaenopsis cochlearis Holttum, Orchid Rev. 72: 408 (1964).

Phalaenopsis corningiana Rchb. f., Gard. Chron., n. s., 11: 620 (1879).

Phalaenopsis cornu-cervi (Breda) Blume & Rchb. f., Hamburger Garten-Blumenzeitung 16: 116 (1860).

Phalaenopsis doweryënsis Garay & Christenson, *Phalaenopsis*. A Monograph, 115 (2001).

Phalaenopsis fasciata Rchb. f., Gard. Chron., n. s., 18: 134 (1882).

Phalaenopsis fimbriata J. J. Sm., Bull. Jard. Bot. Buitenzorg, ser. 3, 3: 300 (1921).

Phalaenopsis floresensis Fowlie, Orchid Digest 57: 35 (1993).

Phalaenopsis fuscata Rchb. f., Gard. Chron., n. s., 2: 6 (1874).

Phalaenopsis ×gersenii (Teijsm. & Binn.) Rolfe, Orchid Rev. 25: 227 (1917).

Phalaenopsis gigantea J. J. Sm., Bull. Dép. Agric. Indes. Néerl. 22: 45 (1909).

Phalaenopsis hieroglyphica (Rchb. f.) H. R. Sweet, Amer. Orchid Soc. Bull. 38: 36 (1969).

Phalaenopsis inscriptiosinensis Fowlie, Orchid Digest 47: 11 (1983).

Phalaenopsis javanica J. J. Sm., Bull. Jard. Bot. Buitenzorg, ser. 2, 26: 77 (1918).

Phalaenopsis kunstleri Hook. f., Fl. Brit. India 6: 30 (1890).

Phalaenopsis lueddemanniana Rchb. f., Bot. Zeitung (Berlin) 23: 146 (1865).

Phalaenopsis luteola Burb. ex Garay, Christenson & Gruss, *Phalaenopsis*. A Monograph, 135 (2001).

Phalaenopsis maculata Rchb. f., Gard. Chron., n. s., 16: 134 (1881).

Phalaenopsis mannii Rchb. f., Gard. Chron. 1871: 902 (1871).

Phalaenopsis mariae Burb. ex Warner & B. S. Williams, Orchid Album 2: t. 80, sub t. 87 (1883).

Phalaenopsis micholitzii Rolfe, Kew Bull. 1920: 130 (1920).

Phalaenopsis modesta J. J. Sm., Icon. Bogor.

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3: 47, t. 218 (1906).

Phalaenopsis pallens (Lindl.) Rchb. f., Ann. Bot. Syst. 6: 932 (1864).

Phalaenopsis pantherina Rchb. f., Bot. Zeitung (Berlin) 22: 298 (1864).

Phalaenopsis pulchra (Rchb. f.) H. R. Sweet, Amer. Orchid Soc. Bull. 37: 1102 (1968).

Phalaenopsis reichenbachiana Rchb. f. & Sander, Gard. Chron., n. s., 18: 586 (1882).

Phalaenopsis robinsonii J. J. Sm., Philipp. J. Sci. 12: 259 (1917).

Phalaenopsis ×**singuliflora** J. J. Sm., Repert. Spec. Nov. Regni Veg. 31: 80 (1932).

Phalaenopsis speciosa Rchb. f., Gard. Chron., n. s., 15: 562 (1881).

Phalaenopsis sumatrana Korth. & Rchb. f., Hamburger Garten-Blumenzeitung 16: 115 (1860).

Phalaenopsis tetraspis Rchb. f., Xenia Orchid. 2: 146 (1868).

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